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ABSTRACT

These materials were designed to be used by life science students for instruction in the application of physical theory to ecosystem operation. Most modules contain computer programs which are built around a particular application of a physical process. Primary production in aquatic ecosystems is carried out by phytoplankton, microscopic plants which move with water currents. The yearly pattern of biological production is in large part controlled by a seasonal cycle of thermal stratification. This module presents a model of primary production in a lake ecosystem. The principal physical, chemical, and biological processes are introduced and the formulation of the model and the mathematical approach used to work with it are described. A final section discusses running the model and modifying its input or boundary conditions so it can be used to simulate a variety of situations. Exposure to numerical analysis and differential equations is a prerequisite to use of the module. (Author/CS)

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SE 033 587

BIOLOGICAL PRODUCTION IN LAKES

by

R.A. Walters and G.F. Carey

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Physical Processes in Terrestrial and Aquatic Ecosystems
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PREFACE

Nutrient and chlorophyll concentrations are the state variables in the model of the primary production in a lake. After a general statement of the problem much of the module is devoted to describing a predictor - corrector method that will give a stable solution for the four coupled, ordinary differential equations. To thoroughly understand the module, the reader should have a lower-division background in biology, and some exposure to numerical analysis and differential equations.

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INTRODUCTION

In this module, we work with a model of primary production in a lake ecosystem. We first introduce the principal physical, chemical and biological processes involved and then describe the formulation of the model and the mathematical approach used to work with it. Finally, we discuss running the model and modifying its input or boundary conditions so it can be used to simulate a variety of situations. This model is, of course, a simplification or idealization of reality but it is more than adequate to understand the processes and how they are represented and synthesized. From that point, an interested person may construct more complicated and realistic models.

A DESCRIPTION OF THE LAKE ECOSYSTEM

Most primary production in both marine and freshwater aquatic systems is carried out by the phytoplankton (in shallow water along shorelines, attached vegetation may be locally important). These small, often microscopic plants move with the water currents and, when given the appropriate levels of temperature and light, produce organic biomass from inorganic nutrients and carbon dioxide. We will examine the operation of this system in freshwater. In lakes, external climatic forcing conditions such as insolation (short-wave solar radiation), air temperature, wind speed, precipitation, and others, produce a seasonal cycle of thermal stratification. The yearly pattern of biological production is in large part controlled by this cycle.

The thermal stratification cycle proceeds as follows. We shall first assume a typical deep, temperate lake where the water temperature remains above 4°C (the temperature of maximum density of freshwater). In the winter and early spring, the lake is cold and nearly isothermal (of constant temperature) with depth. The water density is primarily dependent on temperature so it too is nearly constant. Wind action at the surface can produce water movement and mixing deep into the lake. As insolation and air temperature increase seasonally, the surface water of the lake is heated. Above 4°C, water density is inversely proportional to temperature so the density of the surface water decreases as it warms. The buoyancy of the lower density surface water inhibits mixing with the deeper, colder (and therefore denser) water. By late spring, the lake will have become stratified, with a warm surface layer in which mixing occurs, the epilimnion, separated from the colder, deep water, the hypolimnion, by a zone of steep temperature gradient, the thermocline. The depth of the epilimnion will be set by the balance between heating and the input of mixing energy. The thermocline acts as a barrier to vertical mixing and effectively uncouples the epilimnion from the hypolimnion. We can then, as in this model, think of the lake as a two-compartment system.

The lake will remain stratified through the summer until the seasonal cooling and reduced insolation of the fall. As the water cools and becomes denser at the surface, it will tend to sink and mixing in the epilimnion will increase. Coupled with the decrease in temperature gradient at the thermocline, the mixing will begin to extend into the hypolimnion until, by late fall, the lake is again isothermal.

In lakes where the temperature falls below 4°C, a second stratification cycle may occur. Freshwater density decreases as it cools from 4°C

to the freezing point at 0°C. A cold, low density surface layer with reduced mixing can form. The development of an ice layer on the lake surface will further reduce mixing by uncoupling the wind from the water. It is interesting to note that this stable stratification under the ice prevents complete freezing of the water column and insulates the organisms living in the water. We can ignore this winter stratification cycle for the purposes of this model since primary production is insignificant at these low temperatures and light levels.

In marine systems, the salinity also has an effect on the water density, but the temperature remains the primary controlling factor and the stratification cycle can be modeled in a fashion similar to that in the lake. The surface mixed layer will be deeper and the rate of vertical mixing higher, however, because of tidal and other water currents and a smaller range of seasonal water temperature variation. The effect of the salinity on the temperature-density relationship of water will prevent the winter stratification seen in freshwater.

The water chemistry of the lake varies with the seasonal stratification. Inorganic nutrients produced by the action of macro- and microfauna are released in the bottom sediments into the hypolimnion. During the winter period of high mixing, the surface water also becomes enriched with nutrients. When the water column stratifies, this source of nutrients is cut off from the epilimnion by the greatly reduced mixing. The quantity of nutrients for primary production is thus limited. There may be additional nutrient input from terrestrial runoff, though this is often highest in the season before stratification is fully developed. Man-made wastes, such as sewage effluent, may also be a significant nutrient source. A secondary pulse of nutrient input to the epilimnion is also possible in the early fall

when mixing again increases.

The two major nutrients involved in primary production are nitrogen (usually modeled as nitrate) and phosphorus (modeled as phosphate). Others, such as silicate or carbonate, may have local importance for particular phytoplankton species, while other trace compounds are theorized to have effects but these are not well understood. This model is based on there being a single limiting nutrient in the system. In freshwater ecosystems, phosphate is usually limiting, while in marine systems, because of differences in water chemistry and biological recycling rates, nitrate is most often the limiting nutrient.

The rate of primary production by the phytoplankton is dependent on three major factors: temperature, nutrient concentration, and the amount of sunlight. In the winter, in temperate mid-latitudes, both the low temperature and low insolation limit the primary production, although nutrients are high. Both temperature and insolation increase in the spring but stratification is needed to promote high-production rates. While mixing remains high, the phytoplankton may be carried deeper in the water column than the light can penetrate (the radiation intensity declines exponentially with depth) and the energy produced by photosynthesis may be consumed by metabolism with no net production. The level at which the integrated net production is zero is referred to as the "critical depth." Once the stratification has proceeded to the point that mixing below the critical depth is prevented, and nutrient and light levels are high, a rapid rate of primary production can occur and the phytoplankton population grows quickly, resulting in the spring "bloom."

As the phytoplankton bloom progresses, the nutrient supply is depleted by incorporation into biomass and becomes limiting to the production

rate. The zooplankton that feed on the phytoplankton are growing rapidly in response to the high food supply and can consume the plant biomass faster than it is produced. The phytoplankton population drops to some level which represents a balance between nutrient availability (terrestrial input, mixed across the thermocline, or excreted from zooplankton) and predation by the zooplankton. At the time of fall mixing, there may be a small phytoplankton bloom as the nutrient supply increases, if the light and temperature are high enough.

An actual lake ecosystem includes many factors and interactions not discussed here. These result from differences in climate and weather, lake topography, differences in the species composition of plants and animals in the ecosystem, and the timing of changes in all of these. Although many simplifications and generalizations have been made in the model used here and more complex models have been constructed, no one lake has ever been described and modeled in complete detail. References are provided later for those interested in further reading on lake and marine ecosystems. Some of these will also be useful to anyone wishing to modify or expand on the model presented here.

FORMULATION OF THE MODEL

This model has been formulated using parameter values derived from data from Lake Washington (located adjacent to Seattle, Washington). This is a deep, glacially carved lake which was eutrophic during the period considered. That is, there were an ample supply of inorganic nutrients, such as phosphorus and nitrogen, and a high potential rate of photosynthesis (primary production). The lake undergoes the seasonal stratification cycle

previously described and is not ice-covered in winter.

Under these conditions, the lake is modeled as a two-layer system with all the primary production taking place in the epilimnion. Because of the mixing of the epilimnion, the model assumes that the important properties within it (temperature, nutrient concentration, phytoplankton concentration) are uniform throughout. A major simplification of the model is that the input of solar radiation is also uniform with depth. The primary production rate must then be related to an appropriate mean value of light input. The two-layer model would be a poor representation of an oligotrophic lake (in which nutrient concentrations are low), since there may be considerable variation in phytoplankton concentration in both the epilimnion and hypolimnion, with proportionately more primary production within the latter.

We will use this model to follow the seasonal changes in the concentration of nutrients and the biomass produced by primary production, how they vary in relation to each other and how they may be affected by changes in initial conditions and process rates. Phytoplankton concentrations will be modeled as chlorophyll a concentration; this is a widely used method among aquatic scientists. Phosphorus will be considered the only limiting nutrient as is usually the case in eutrophic, freshwater systems (nitrogen is usually limiting in marine systems, however). As noted above, concentrations and temperatures are modeled as uniform within each layer and all primary production is assumed to occur in the epilimnion. The water temperatures are built into the program but the mixing coefficient between layers is specified as an input variable.

The most significant departure of this model from reality is the omission of any terms related to the consumption of the phytoplankton by

zooplankton or other predators. Such additional equations would reduce the rate of increase of phytoplankton biomass and increase the availability of nutrients (via recycling through zooplankton excretion and defecation). This omission does not change the gross pattern of a phytoplankton bloom and nutrient depletion but it does alter the relative and absolute values of the rates and concentrations. As one becomes familiar with the model, additional complexity may be added, as noted later in the section Advanced Modeling.

The model can be thought of as consisting of two one-cubic-meter boxes, one in the epilimnion, Box_E, and one in the hypolimnion, Box_H. Some material is generated inside a box (e.g. phytoplankton growth and reproduction), some is lost from the box (e.g. respiration or sinking), and some is added to it. The latter operation is somewhat tricky since, when material is added, it is added to an entire one-meter-wide column in a strata and must be apportioned to a box. For example, consider the CLOAD parameter in equation set (1) below. This represents chlorophyll *a* added to the entire epilimnion from streams. However, Box_E is only one meter high, so that only $CLOAD/H_E$ (where H_E is the depth of the eplimnion) is added to Box_E. Similarly, the $SINK_H$ parameter in equation set (1) represents not only sinking out of Box_H but addition to Box_H of chlorophyll *a* sinking from the epilimnion. Since H_E meters of chlorophyll *a* sink into H_H meters in the hypolimnion, only H_E/H_H proportion of $SINK_E$ is added to Box_H.

The time rate of change of chlorophyll *a* and phosphorus in the two layers can be written as four coupled differential equations as follows:

$$\left.\begin{aligned}
\frac{dC_E}{dt} &= PROD - RES_E - SINK_E - CMX + \frac{CLOAD}{H_E} - \frac{RHYD}{H_E} C_E \\
\frac{dP_E}{dt} &= VP_E - PMX + \frac{PLOAD}{H_E} - \frac{RHYD}{H_E} P_E \\
\frac{dC_H}{dt} &= -RES_H - SINK_H + CMX \frac{H_E}{H_H} \\
\frac{dP_H}{dt} &= VP_H + PMX \frac{H_E}{H_H} + S/H_H
\end{aligned}\right\} \qquad (1)$$

where C, P are chlorophyll a and phosphorous concentrations (kg/m^3); the subscripts E, H denote epilimnion and hypolimnion; H_E and H_H are epilimnion and hypolimnion depths; PROD is the primary production rate ($kg\ C/m^3$-sec); RES is the respiration rate ($kg\ C/m^3$-sec); SINK is the removal rate due to sinking ($kg\ C/m^3$-sec); CMX and PMX are the mixing rates for chlorophyll a and phosphorus between the layers (kg C or kg P/m^3-sec); CLOAD and PLOAD are the chlorophyll a and phosphorus loading from river and other sources (kg C or kg P/m^2-sec); RHYD is the hydraulic loading rate due to dilution as water passes through the lake (m/sec); VP is the nutrient uptake rate ($kg\ P/m^3$-sec); and S is the rate of transfer of phosphorus at the sediment ($kg\ P/m^2$-sec). Detailed expressions for some of these terms may be written. The production has the general form:

$$PROD = p_{max}(L)\ \exp\{-(T_E - T_{opt})^2/25\}\left(\frac{P_E}{P_E+K_P}\right) C_E \qquad (2a)$$

where p_{max} is the maximum possible production rate, L is a light-intensity factor, T_{opt} is the optimum growing temperature, and $P_E/(P_E+K_P)$ is the

nutrient dependence on growth. If more than one nutrient is being modeled, additional dependencies of this form can be added as a multiplicative series.

Similarly, the respiration rates have the form

$$RES_E = .1\ p_{max}\ \exp\{-(T_E-T_{opt})^2/25\}\ C_E$$

and

$$RES_H = .1\ p_{max}\ \exp\{-(T_H-T_{opt})^2/25\}\ C_H \qquad (2b)$$

so that respiration is 10% of the maximum production at a given temperature.

The sinking rate in the layers (E and HO is simply

$$SINK_E = (W_E/H_E)C_E$$

and

$$SINK_H = (W_H/H_H)C_H - (SINK_E)(H_E/H_H)C_E \qquad (2c)$$

where W is the sinking velocity of the phytoplankton. Mixing rates are given by

$$CMX = K(C_E-C_H)$$

and

$$PMX = K(P_E-P_H) \qquad (2d)$$

where K is the mixing coefficient (sec^{-1}).

The nutrient uptake rate is assumed to be proportional to the net primary production:

$$VP_E = RATIO(RES_E\text{-}PROD)$$

and

$$VP_H = RATIO(RES_H)\ ,$$

where RATIO is the phosphorus to chlorophyll a ratio of the phytoplankton (kg P/kg C). A summary of the input parameters and their range of variation is given in the Input Table in the User's Guide for program LAKE. Two additional parameters, light intensity L and the exchange (or mixing) coefficient K are built into the program and take on the ranges

$$0.01639 \leq L \leq 0.508 \quad \text{and}$$
$$1.1574\times10^{-8} \leq K \leq 1.1574\times10^{-6} \ .$$

Once these parameters are specified, we are left with four coupled equations for the two chlorophyll a and the two phosphorous values as a function of time.

NUMERICAL AND APPROXIMATE ANALYSIS

The system of governing differential equations described by eq. 1, together with appropriate known initial values of chlorophyll a and phosphorous concentrations in the two layers, constitutes an initial-value problem to be solved for C_E, C_H, P_E and P_H as functions of time. The complicated production and respiration terms depend nonlinearly on the unknown chlorophyll a and phosphorous values at any given time and prohibit analytic solution. Furthermore, the objective here is to develop an analysis and program that will be a basis for alternative models utilizing different relationships for the important terms in eq. 1. Consequently, we are interested in solving a more general problem that may be expressed in the form

$$\frac{d\underset{\sim}{\phi}}{dt} = \underset{\sim}{f}(\underset{\sim}{\phi}) \qquad (3)$$

where $\underset{\sim}{\phi}(t) = \{\phi_i(t)\} \equiv \{C_E(t), P_E(t), C_H(t), P_H(t)\}$ is the solution vector, and $\underset{\sim}{f}(\underset{\sim}{\phi}) = f_i(\underset{\sim}{\phi}(t))$ represents a general vector of right-hand-side expressions, including that given in eq. 1.

To determine $\underset{\sim}{\phi}(t)$ from initial conditions and satisfying eq. 3 to a desirable degree of approximation, a variety of numerical approximation strategies are possible. The simplest of these involve some form of finite difference approximation in time, utilizing the equation and known values at the start of a time increment to estimate the solution at the end of the timestep. In this fashion, the equations can be systematically integrated in time. For example, perhaps the simplest scheme is due to Euler, and replaces eq. 3 by

$$\frac{\underset{\sim}{\phi}(t_i+\Delta t) - \underset{\sim}{\phi}(t_i)}{\Delta t} = \underset{\sim}{f}(\underset{\sim}{\phi}(t_i)) \quad , \quad \text{given } \phi_0 = \underset{\sim}{\phi}(t=t_0) \quad . \tag{4}$$

Then

$$\underset{\sim}{\phi}(t_i+\Delta t) = \underset{\sim}{\phi}(t_i) + \Delta t \underset{\sim}{f}(\underset{\sim}{\phi}(t_i)) \tag{5}$$

provides a general algorithm. The error by Taylor Series arguments is of order $(\Delta t)^2$.

However, the application of numerical approximating techniques to initial value problems is seldom as straightforward as this suggests. The problem becomes complicated by questions of accuracy, consistency, and stability. These topics and the mathematical foundations of the associated numerical techniques are beyond the scope of this module. An attempt to solve eq. 1 with a direct, explicit scheme, such as that in eq. 4, gives an indication of the issues involved; one class of techniques termed Runge-Kutta methods ((4), A. Ralston, p. 190), integrates the differential equation in

an explicit sense as in eq. 4 but more accurately, using several derivative estimates to step forward. In the particular problem of interest here, there is, in a sense, a competition between the production and respiration terms coupled through the right-hand side of the system. The numerical scheme functions adequately until approximately one-third of the annual cycle is completed. At this point, the phosphorus has been depleted, and the derivative estimates in the Runge-Kutta scheme cannot be adequately obtained. The solution oscillates (into negative values), becomes numerically unstable, and the scheme fails. Reducing the timestep or introducing a higher order approximation of the same form only delays the inevitable.

Accordingly, an alternative approach must be sought in which these instabilities are circumvented. An implicit scheme motivated by the Crank-Nicolson approach used successfully for parabolic partial differential equations was implemented in conjunction with a predictor-corrector technique for this biological production system. The above-mentioned difficulties do not arise and this analysis provides the basis for the associated computer program. Thus the scheme actually used combines an implicit approach with an explicit predictor-corrector scheme. Let us first briefly describe these approaches separately and then the modified scheme used in the primary production model.

In a simple implicit approach function f is evaluated iteratively at the mean value between timesteps. Equation 3 implies that on differencing in time between timesteps j and j+1,

$$\frac{\underset{\sim}{\phi}^{j+1} - \underset{\sim}{\phi}^{j}}{\Delta t} = f\left(\frac{\underset{\sim}{\phi}^{j} + \underset{\sim}{\phi}^{j+1}}{2}\right) \quad . \tag{6}$$

In general $\underset{\sim}{f}$ will be nonlinear and a nonlinear algebraic technique will be needed to solve for $\underset{\sim}{\phi}^{j+1}$. In a predictor-corrector scheme, the first step is usually an explicit step as in the Euler or Runge-Kutta type methods. This determines an estimate $\underset{\sim}{\phi}^{j+1}$ for the solution at the end of the step. The corrector stage iteratively updates this estimate to improve the solution. Thus we have a simple example at step (j+1),

$$\text{Predictor:} \quad \underset{\sim}{\phi}_0^{j+1} = \underset{\sim}{\phi}^{j} + \Delta t \, \underset{\sim}{f}(\underset{\sim}{\phi}^{j}) \tag{7}$$

$$\text{Corrector:} \quad \underset{\sim}{\phi}_k^{j+1} = \underset{\sim}{\phi}^{j} + \Delta t \, \underset{\sim}{f}\left(\frac{\underset{\sim}{\phi}_{k-1}^{j+1} + \underset{\sim}{\phi}^{j}}{2}\right) , \quad k=1 \ldots , n \ .$$

The iteration ceases when $||\underset{\sim}{\phi}_{k+1}^{j+1} - \underset{\sim}{\phi}_k^{j+1}||$ is within a prescribed tolerance.

The scheme we have used may be categorized as a particular hybrid of the general class of predictor-corrector techniques described by (7) and the implicit approach of (6). This is convenient here as we can exploit the structure of the individual equations in (1). Consider the chlorophyll a equation in the epilimnion and the first timestep:

$$\frac{dC_E}{dt} = f_1(C_E, P_E, C_H, P_H) \ . \tag{8}$$

As the first dependent variable C_E appears linearly in the function f_1, an implicit scheme in C_E can be used directly with P_E, C_H, P_H, set at the starting values for the beginning of the step. Then we have, on setting $(C_E^{\,j} + C_E^{\,j+1})/2$ for C_E in $f_1(C_E)$,

$$C_E^{j+1} - C_E^{j} = \Delta t \left[\text{PROD}(P_E^j, \frac{C_E^j + C_E^{j+1}}{2}) - \text{RES}_E(\frac{C_E^j + C_E^{j+1}}{2}) - \text{SINK}_E(\frac{C_E^j + C_E^{j+1}}{2}) \right.$$
$$\left. - \text{CMX}(\frac{C_E^j + C_E^{j+1}}{2}, C_H^j) + \frac{\text{CLOAD}}{H_E} - \frac{\text{RHYD}}{H_E}(\frac{C_E^j + C_E^{j+1}}{2}) \right] \tag{9}$$

Transferring terms in C_E^{j+1} to the left-hand side, the resulting linear equation is directly solved to yield an estimate of C_E^{j+1}.

Consider now the phosphorous equation in the epilimnion,

$$\frac{dP_E}{dt} = f_2(C_E, P_E, C_H, P_H) \quad . \tag{10}$$

We use the "most recent information" C_E^{j+1} and replace C_E by $(C_E^j + C_E^{j+1})/2$. The starting values of C_H^j and P_H^j are known and used directly in f_2. As P_E appears nonlinearly through the production expression, the convenient implicit approach used for the C_E equation is not applicable. Instead an explicit (Euler) predictor is used with P_E replaced by P_E^j in f_2, yielding

$$P_E^{j+1} = P_E^j + \Delta t\left[VP_E\left(P_E^j, \frac{C_E^{j+1}+C_E^j}{2}\right) - PMX(P_E^j, P_H^j) + \frac{PLOAD}{H_E} - \frac{RHYD}{H_E} P_E^j\right] \quad . \tag{11}$$

Depending on the degree of nonlinearity, one may wish to iteratively correct this equation using $(P_E^j + P_E^{j+1}{}_*)/2$ for P_E in f_2, where $P_E^{j+1}{}_*$ is the current-corrector estimate of P_E^{j+1}.

Again using the most recent information, (with C_E and P_E replaced by midstep averages) the equation for chlorophyll a in the hypolimnion may next be differenced. As C_H appears linearly, the direct implicit scheme analogous to eq. 9 may be used,

$$C_H^{j+1} = C_H^j + \Delta t\left[-RES_H\left(\frac{C_H^j + C_H^{j+1}}{2}\right) - SINK_H\left(\frac{C_H^j + C_H^{j+1}}{2}, \frac{C_E^j + C_E^{j+1}}{2}\right) - \frac{H_E}{H_H} CMX\left(\frac{C_E^j + C_E^{j+1}}{2}, \frac{C_H^j + C_H^{j+1}}{2}\right)\right] \tag{12}$$

On transferring terms in C_H^{j+1} to the left, the resulting linear equation is solved directly.

Finally, the equation for phosphorous concentration in the hypolimnion is differenced in a similar manner to the equation for P_E. However, the

equation is linear since the production term is absent:

$$P_H^{j+1} = P_H^j + \Delta t \left[VP_H \left(\frac{C_E^j + C_E^{j+1}}{2} \right) - \frac{H_E}{H_H} PMX \left(\frac{P_E^j + P_E^{j+1}}{2}, \frac{P_H^j + P_H^{j+1}}{2} \right) + \frac{S}{H_H} \right] \tag{13}$$

and can be solved by transferring C_H^{j+1} terms to the left.

Having completed one "sweep" through the differenced system, the procedure of eqs. 9, 11, 12 and 13 is repeated using now the mid-step values of all dependent variables and "most recent information" as it becomes available within a given "sweep." A couple of such corrector sweeps have been sufficient to produce accurate results for calculations with moderate timesteps. Related results for sample problems are indicated in the following section.

Remark: Numerical results indicate that the phosphorous equations appear to be less sensitive and converge rapidly. This suggests that an alternative scheme, whereby the equations for P_E and P_H are first considered and less frequently updated, might be more efficient.

RESULTS

Example Problem

We consider a stratified temperate lake with upper layer (epilimnion) of depth 10 m and adjacent lower layer (hypolimnion) of depth 40 m. The governing mass transfer relations for chlorophyll a and phosphorus are presented in eq. 1, and require specification of related parameters and functions appearing in the right-hand-side expression. For clarity, in this illustrative example, we assume there is no influx or efflux of chlorophyll a and phosphorus via rivers or other means, so that the loading factors CLOAD

and PLOAD are zero. Similarly, the hydraulic loading rate (RHYD) due to dilution as water passes through the lake is assumed zero, and there is assumed to be no transfer of phosphorus to or from the sediment so that RSED = 0. The phytoplankton are presumed to form gas vacuoles so that the sinking speed W may be taken to be zero, and the sink term (SINK) is consequently zero.

The primary production rate (RPROD) has been experimentally determined at 20°C to be 0.28×10^{-5}, and the nutrient uptake rate is proportional to the net primary production with proportionality constant (RATIO) 3. The phosphorus half-saturation constant is determined as 3×10^{-6} kg/m^3. Initially, at reference time t = 0, the chlorophyll a and phosphorous concentrations are ICHL = 3×10^{-6} kg/m^3 and IPHOS = 7×10^{-5} kg/m^3, respectively. The evaluation of the chlorophyll a and phosphorous concentrations in each layer is described by integrating the coupled system of eq. 1 in time, here over a period of 200 days with fixed timestep of one-half day.

The first graph (Fig. 1) depicts the production term (eq. 2a) over the period of interest. At the beginning (winter and early spring), the phytoplankton concentration is low and nutrient concentration is at its yearly maximum. Since temperatures and light intensity are low, primary production is low. As described earlier, stratification begins and a rapid growth of the phytoplankton occurs in the epilimnion. This is indicated in the figure by an abrupt increase in production. However, the available nutrient in the epilimnion is swiftly depleted and production drops markedly. The associated respiration in the epilimnion (see eq. 2b) is graphed in Fig. 2, showing a similar marked increase but more moderate decline during the spring-to-fall period. The detailed solution profiles for chlorophyll a

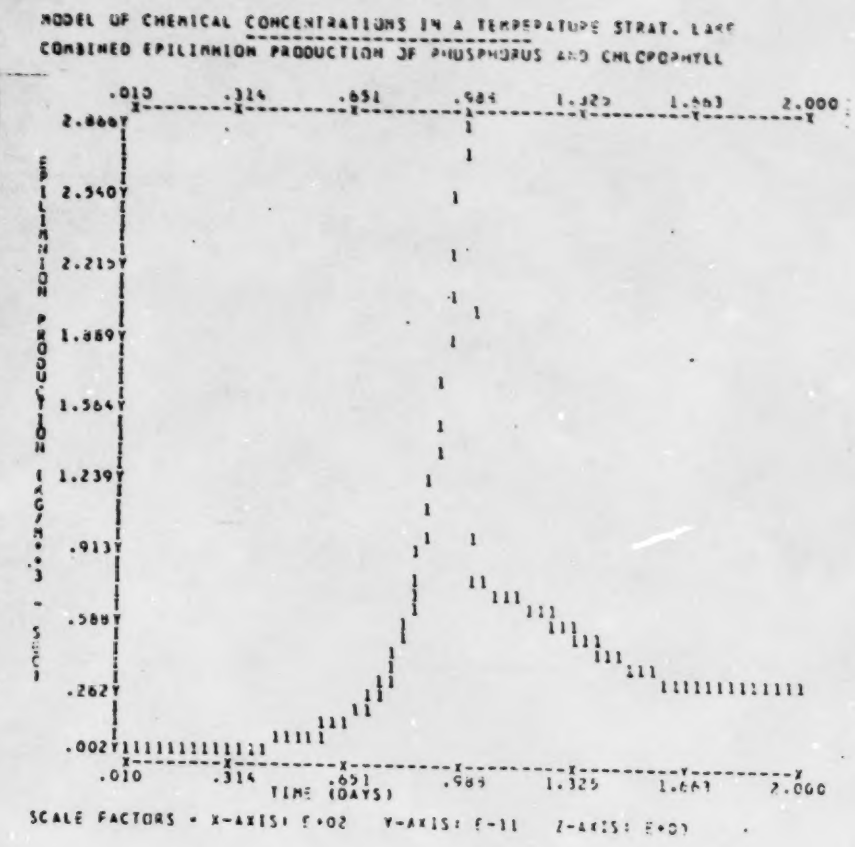


Figure 1

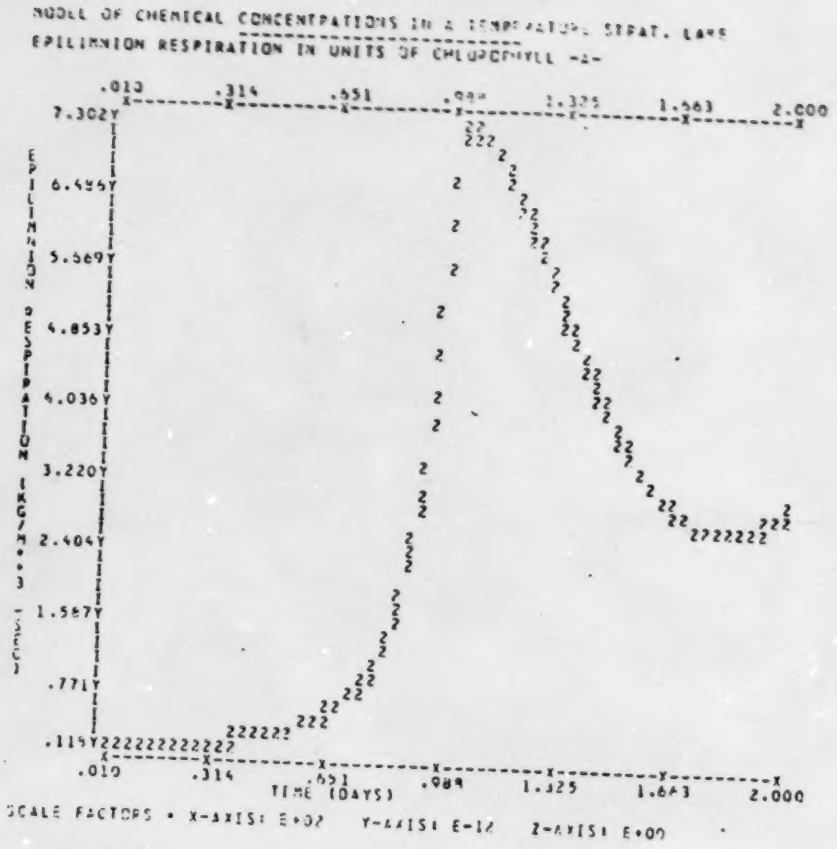


Figure 2

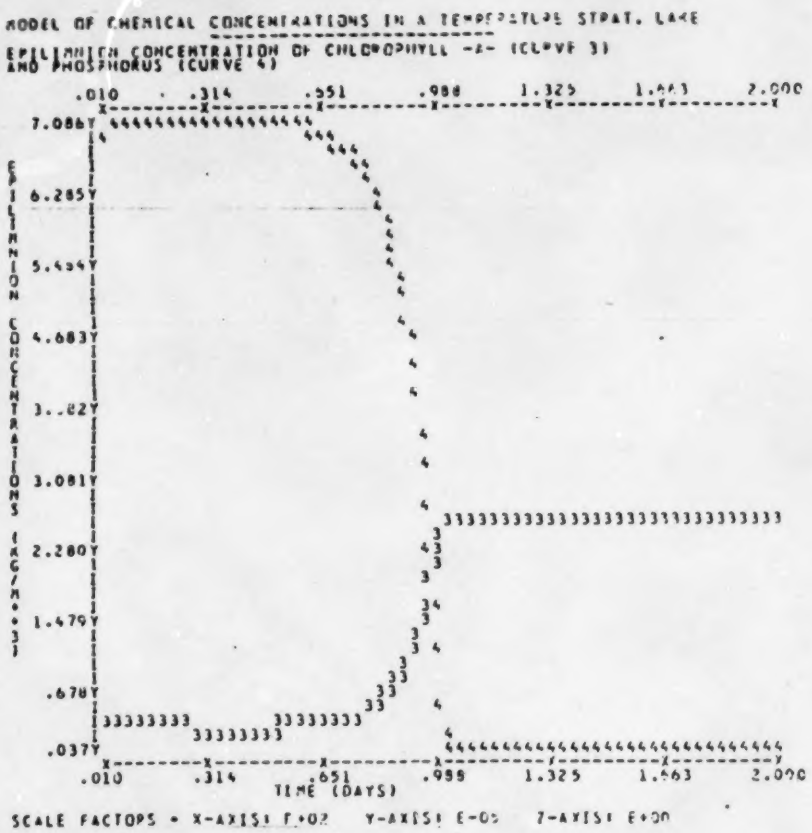


Figure 3

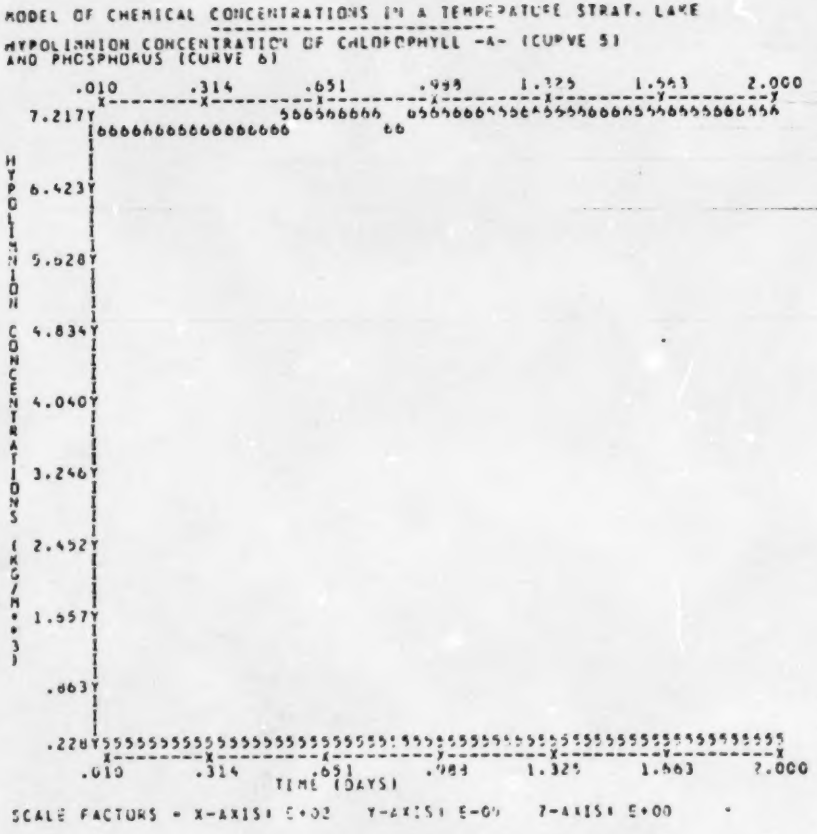


Figure 4

and phosphorus in the upper layer are given in Fig. 3. The phosphorous concentration falls from its yearly maximum to a minimum value during the period of high production, and the chlorophyll a rises from a minimum to a steady maximum concurrently. Results for C_H and P_H in the final figure (Fig. 4) reflect the confinement of production to the euphotic zone which is of the order of epilimnion depth, and the fact that on stratification, mixing through the thermocline is small.

ADVANCED MODELING

In this section, we wish to set out guidelines for modifying this analysis to include other processes and to change the existing mathematical relationships contained in the model. It is important that the section entitled "Numerical and Approximate Analysis" be read before proceeding with this section.

While making modifications, one must be concerned with two general problem areas: (1) introducing large changes in the C and P values over a period of a timestep or less, and (2) not preserving a certain symmetry between the C and P equations which leads to a non-conservative system. In the first case, large changes cause the truncation errors in the finite difference approximations to become important with the result that accuracy becomes poor. (For instance, study the effect of increasing p_{max} by a factor of 10.) Terms which have been added or modified may be compared in magnitude with p_{max} C which is of the order of the maximum rate of change of C. Typically, maximum changes in the dependent variables per timestep are about 0.1%. If it is found that the system becomes unstable due to large changes in the variables, the timestep can be decreased as much as is necessary to

reduce the changes to a reasonable magnitude. Automatic stepsize adjustment has not been included in the program.

The second general area concerns the mathematical formulation of the different processes which affect the dependent variables C and P. In particular, it is necessary to discriminate between linear and non-linear functions of these variables. For instance, as we noted earlier, the production term is linear in C so that we may write an implicit prediction for C. However, this term is nonlinear in P, so that when the predictor for P is written, it appears natural to write this term implicitly as

$$\text{PROD}\Big|_{\text{at } t_0} + \frac{\partial \text{PROD}}{\partial P}\Big|_{\text{at } t_0} \Delta P$$

where $\Delta P = (P^{j+1} - P^j)/2$.

However, now the production term is not the same in both the C and P equations so that when C and P are transferred back and forth during growth and mortality, some C or P may be "lost" or "gained" in the system. That is, the numerical differencing algorithm is not conservative! To circumvent this difficulty the production term is written implicitly when solving for C, and explicitly when solving for P so that no material is gained or lost in the system due to approximation errors in this term. The general rule then becomes: if the term is linear in the variable being solved for, write the term implicitly in the predictor for accuracy and stability, e.g.,

$$\frac{C^{j+1}+C^j}{\Delta t} = g(P)\ \left(\frac{C^{j+1}+C^j}{2}\right) \quad \text{for production.}$$

If the term is nonlinear, write the term explicitly to avoid the aforementioned

errors, e.g.,

$$\frac{P^{j+1}-P^j}{\Delta t} = C\left(\frac{P^j}{P^j+K_p}\right) \quad \text{for production.}$$

A natural extension of this model would be to include more than one nutrient, more than one type of phytoplankton, or higher trophic levels such as herbivores. The analysis and program can be readily extended with little modification to include additional equations.

For each additional nutrient, two equations are added to the system and the additional dependencies are included in the production term. For example, including nitrogen N:

$$PROD = PROD_{OLD}\left(\frac{N_E}{N_E+K_N}\right) \quad .$$

The equations for $\frac{dN_E}{dt}$ and $\frac{dN_H}{dt}$ would resemble the phosphorous equations with P replaced by N, P-loading changed to N-loading, and RP changed to RN, the nitrogen to chlorophyll a ratio.

To model an additional type of phytoplankton, two additional equations for C are needed and the parameters T_{opt}, K_p, etc. would be different so that the organisms compete.

For model grazing, terms could be added to the C equations and appropriately included in the approximate analysis.

REFERENCES

1. Edmondson, W.T. 1972. The present condition of Lake Washington. International Association of Theoretical and Applied Limnology, Proceedings 18:284-291.

2. Fleming, W.M. 1975. A model of the phosphorous cycle and phytoplankton growth in Skaha Lake, British Columbia. International Association of Theoretical and Applied Limnology, Proceedings 19:229-240.

3. Imboden, D. 1974. Phosphorous model of lake eutrophication. Limnology and Oceanography 19:297-304.

4. Ralston, A. 1970. A First Course in Numerical Analysis. McGraw-Hill Book Company.

For further reading:

A series of papers dealing with nutrient-phytoplankton-zooplankton models in the open ocean are listed. They utilize the same basic stratification cycle, a single limiting nutrient, and include a formulation for predation on the phytoplankton. They do not include the addition and/or dilution factors of rivers and sediments that a lake ecosystem would need. The last reference includes the complexity of the size structure of the populations.

1. Steele, J.H. 1974. The Structure of Marine Ecosystems. Harvard University Press. 128 pp.

2. Landy, M.R. 1976. The structure of marine ecosystems: an alternative. Marine Biology 35:1-7.

3. Steele, J.H. and B.W. Frost. 1977. The structure of plankton communities. Phil. Trans. Royal Soc. Lond. 280:485-534.

Additional references useful for understanding plankton ecology and some of the governing equations, plus added complexities, are:

4. Fogg, G.E. 1975. Algal Cultures and Phytoplankton Ecology. University of Wisconsin Press. 175 pp.

5. Russell-Hunter, W.D. 1970. Aquatic Productivity. Macmillan. 306 pp.

6. Parsons, T.R., M. Takahashi and B. Hargrave. 1977. Biological Oceanographic Processes. Pergamon. 332 pp.

The former two deal with freshwater as well as marine systems.

ACKNOWLEDGMENTS

The authors express their appreciation to D. Winter for his suggestions; to L. Anderson for assisting with the programming; to R. Wells for his contributions to the biological background and general commentary; and to L. Gales for his careful work coordinating the overall programming, documentation and computational aspects.

COMPUTER PROBLEMS

Program LAKE is described in detail in the section titled "User's Guide for Program LAKE." It contains a line-printer graphics subroutine named PRNT3D (Gales, 1978) which displays all of the output generated by the program. In each exercise, the user must input certain parameter values according to the rules and restrictions listed in the user's guide. Sometimes, solutions may fail to converge or numerical errors may abort the program even when all input parameters remain within allowed limits. In these cases, one must either increase JSTEP (the number of steps per integration) or slightly alter the input parameters in order to insure convergence.

1. In the first sample run (plot 3), the chlorophyll a concentration in the epilimnion rises until about day 100 and then remains constant. Can you force the chlorophyll a concentration to fall after it peaks?

2. The phytoplankton bloom seems to peak around day 90-100 and would appear to be largely controlled by the light and temperature cycles built into the program. Can you significantly change the peak bloom time using the input parameters?

3. The phosphorus in the epilimnion tends to sink to very low, but non-zero, levels after the phytoplankton bloom. If it went to zero, the program would respond with an error message (see error number 15 in the user's guide). Can you force the phosphorous level to 0?

4. Can you reduce the phosphorous levels in the hypolimnion? Can you increase the chlorophyll a concentrations in the hypolimnion? Do the levels remain approximately constant or can you cause them to vary over time?

5. One way of cleaning turbid water is to let everything settle out. Use maximum sinking rate and observe the response of C and P over an extended (NDAYS=300) period of time. Where has all the flora gone? Phosphorus?

USER'S GUIDE FOR PROGRAM LAKE

Identification

LAKE - A program which simulates the evolution of chlorophyll a and phosphorous concentrations in the upper and lower layers of a stratified lake.

Authors - L. Gales, R.A. Walters and L. Andersen, Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle. July 1979.

Purpose

Program LAKE is the computer supplement to the module "Biological Production in Lakes," by R.A. Walters and G.F. Carey. It is designed to study the evolution of chlorophyll a and phosphorous concentrations in the upper and lower layers of a temperate stratified lake. Conservation of mass for phytoplankton and nutrient concentrations lead to a coupled system of four differential equations for $C_E(t)$, $P_E(t)$, $C_H(t)$ and $P_H(t)$ respectively, where C stands for chlorophyll a, P stands for phosphorus, and E and H subscripts stand for epilimnion and hypolimnion, respectively. Numerical techniques are applied to integrate the equations in time using implicit and conservative differencing schemes where appropriate.

Operation

The user controls program LAKE by means of a number of input parameters which prescribe the physical and biological scenario for the simulation and also the format and selection of output. Values not supplied by the user are automatically provided by the program.

The physical and biological parameters, which are described in detail in the section labeled Input, include such things as epilimnion and

hypolimnion depths, various loading and exchange rates, initial chemical concentrations, and the start and duration of simulation. There are three important parameters, however, which are built into the program and cannot be changed. These are the hypolimnion temperature (which remains constant), the epilimnion temperature, and the light intensity. The latter two are modeled as sinusoidal functions which start at low levels in January, move to high levels in June-July, and return to low levels in December. The only control the user has over these variables is the starting time of simulation.

The user controls the selection of output by means of an option list named OPLIST. Each option in the list may take on the values 1 through 4 (a null option is specified by zero) and the list may contain up to four unique elements. The options are:

Option 1: plot epilimnion production vs. time

Option 2: plot epilimnion respiration vs. time

Option 3: plot epilimnion chlorophyll a and phosphorous concentrations vs. time

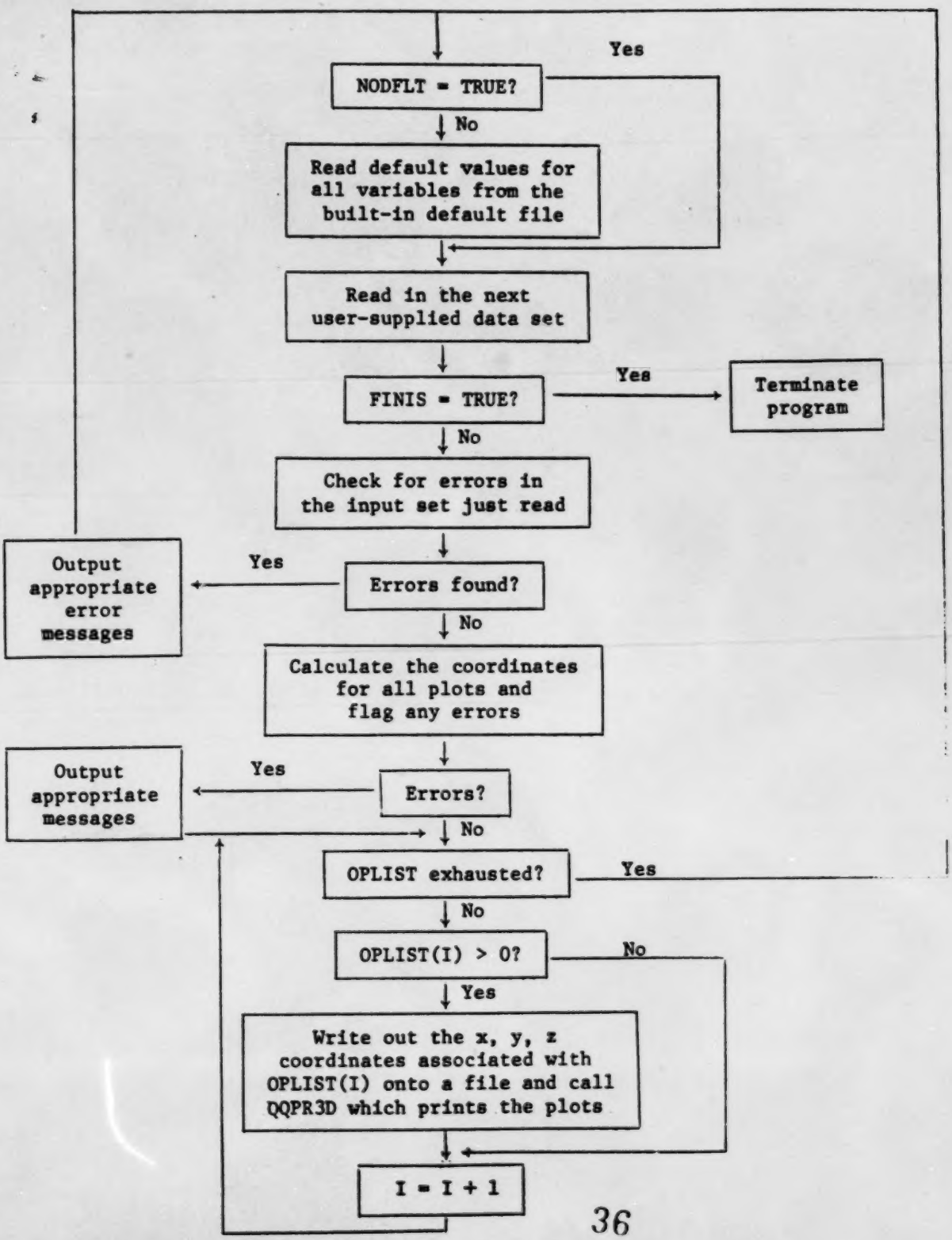
Option 4: plot hypolimnion chlorophyll a and phosphorous concentrations vs. time.

For example, OPLIST = 2, 1, 4 invokes options 2, 1, and 4 in a single run.

LAKE calls a printer plot package named PRNT3D to generate the plots. The plot formats (e.g., size, shape, scaling, etc.) are controlled by a large number of user-assignable parameters which are described in the User's Guide for subroutine PRNT3D (Gales, 1978). These parameters may be included along with the above mentioned input for LAKE; however, LAKE itself assigns default values which are adequate for most purposes.

Program Organization

The program is organized around the following flow chart:



Input

All input is handled by a format-free input package (Gales and Anderson, 1978) which permits a user to assign values to variables by a "name=value" convention. Not all variables need be explicitly assigned by the user, however, as unassigned variables automatically assume default values. The input consists of any number of data sets, each of which is terminated by a dollar sign ($). Comments in an input set are enclosed within slashes (/). Each data set may generate a number of printer plots.

The input for LAKE is divided into three classes: (a) variables having physical or biological significance or related to program options: EDEPTH, HDEPTH, CLOAD, PLOAD, RPROD, SINK, RATIO, RHYD, RSED, PSAT, ICHL, IPHOS, ITIME, NDAYS, JSTEP, and OPLIST; (b) variables which control certain program operations, such as program termination or the handling of default input: IPRINT, ECHO, NODFLT, and FINIS; and (c) variables which control the printer plots (default values are in parentheses): XMIN(0), XMAX(0), YMIN(0), YMAX(0), ZMIN(0), ZMAX(9), XRICH(0), YRICH(0), DFAULT(0), QQPRNT(.F.), AVE(.F.), INT2D(.F.), NX(60), NY(45), and ZMAP(0,1,2,3,4,5,6,7,8,9). The variables in the first two classes are explained in the following INPUT TABLE, whereas the printer plot variables are explained in the User's Guide for PRNT3D (Gales, 1978). Names or symbols in parentheses below some of the input variable names refer to the symbols used in the equations in the text.

INPUT TABLE

Name	Type and Dimensions	Range Limits	Description
EDEPTH (H_E)	Real	$\geq$ 5.0	Epilimnion depth, in meters. Default value is: EDEPTH = 10.
HDEPTH (H_H)	Real	$\geq$ 5.0	Hypolimnion depth, in meters. Default value is: HDEPTH = 40.
CLOAD	Real	$\geq$ 0	Chlorophyll a loading, in kg/m^2-sec. Default value is: CLOAD = 0.
PLOAD	Real	[0, 1.3×10^{-4}]	Phosphorous loading, in kg/m^2-sec. Default value is: PLOAD = 0.
RPROD (P_{max})	Real	[1.2×10^{-6}, 1.2×10^{-5}]	Primary production rate, in sec^{-1} Default value is: RPROD = 2.8E-6.
SINK	Real	[0, 6×10^{-6}]	Sinking speed, in meters/sec. Default value is: SINK = 0.
RATIO	Real	[1, 4]	Ratio of phosphorus to chlorophyll a. Default value is: RATIO = 3.
RHYD	Real	[0, $1.2\ 10^{-6}$]	Rate of hydraulic loading, in meters/sec. Default value is: RHYD = 0.
RSED (S)	Real	[0, 1.2×10^{-5}]	Rate of sediment regeneration of phosphorus, in kg/m^2-sec. Default value is: RSED = 0.

Input Table (cont.)

Name	Type and Dimensions	Range Limits	Description
PSAT (K_p)	Real	$[10^{-6}, 3.1\times10^{-5}]$	Phosphorous half-saturation constant, in kg/m^3. Default value is: PSAT = 3E-6.
ICHL	Real	$[0, 5\times10^{-5}]$	Initial chlorophyll *a* concentration, in kg/m^3. Default value is: ICHL = 3E-6.
IPHOS	Real	$[0, 10^{-4}]$	Initial phosphorous concentration, in kg/m^3. Default value is: IPHOS = 7E-5.
ITIME	Real	[0, 365]	Initial (starting) time for simulation, in Julian days. Default value is: ITIME = 0.
NDAYS	Integer	[0, 365]	Number of days to run simulation. Default value is: NDAYS = 100.
JSTEP	Integer	[0, 999]	Steps per day used to solve differential equation. Default value is: JSTEP = 2.
OPLIST	Integer (4)	0 - 4	A list of up to four options which select the output. The options are as follows: 1. plot epilimnion production vs. time 2. plot epilimnion respiration vs. time 3. plot epilimnion chlorophyll *a* and phosphorous concentrations vs. time

Input Table (cont.)

Name	Type and Dimensions	Range Limits	Description
OPLIST (cont.)			4. plot hypolimnion chlorophyll a and phosphorous concentrations vs. time. 0: ignore Default values are: OPLIST = 1, 0, 0, 0
IPRINT	Logical	.F., .T.	A logical value which causes the current values for all input variables (default as well as current user input) to be printed. Default value is: IPRINT = .F.
ECHO	Logical	.F., .T.	A logical value which causes the user's input to be echoed if ECHO = .T., or suppresses echoing if ECHO = .F. Default value is: ECHO = .T.
NODFLT	Logical	.F., .T.	A logical value which suppresses the input of default values if NODFLT = .T. Default value is: NODFLT = .F.
FINIS	Logical	.F., .T.	A logical value which causes program termination if and only if FINIS = .T. Default value is: FINIS = .F.

The last four variables deserve special mention.

1. The logical variable IPRINT controls the output of all input variables which are currently in effect (default values as well as those specified in the current input set). Setting IPRINT=TRUE (or T or .T.) displays the current values for all input variables; setting IPRINT=FALSE (or F or .F.) suppresses the display.
2. The logical variable ECHO controls the echoing of the input cards. Setting ECHO=TRUE causes the subsequent input set to be echoed; setting ECHO=FALSE suppresses the echo for the subsequent input set.
3. The logical variable NODFLT can be used to inhibit the automatic assignment of default values to input variables. If NODFLT is set TRUE in the current input set, then the current input set is assigned default values as usual, but all subsequent input sets merely accumulate more input values. In effect, the input values which exist after the i-th input set is read, become the default values for the (i+1)-th input set. The standard default values may then be restored by setting NODFLT=FALSE, but, again, the effects of this change are delayed until the next input set is read. To a limited extend, NODFLT permits a user to set up his own default values and can be very useful for executing a number of input sets which differ only in a few parameters. Consider the following example in which a user wishes to make a number of runs which differ only in terms of the initial concentrations of chlorophyll a and phosphorus:

```
/INPUT SET 1:  THE FOLLOWING VALUES BECOME THE DE FACTO/
/DEFALUT VALUES FOR ALL SUBSEQUENT INPUT SETS:        /
    NODFLT = TRUE, EDEPTH = 10, HDEPTH = 40, CLOAD = 0,
    PLOAD = 0, RPROD = 2.8E-6, SINK = 0, RATIO = 3,
    RHYD = 0, RSED = 0, PSAT = 3E-6, ITIME = 0
    NDAYS = 100, JSTEP = 2, ICHL = 3E-6, IPHOS = 7E-5, $

/NOW CHANGE ICHL AND IHPOS only                       /
    ICHL = 3.2E-6, IPHOS = 7.1E-5, $
```

```
/CHANGE THEM AGAIN                                          /
    ICHL = 2.7E-6, IPHOS = 7E-5, $

/AND AGAIN                                                  /
    ICHL = 2.4E-6, IPHOS = 6.1E-5, $

/NOW STOP                                                   /
    FINIS = TRUE, $
```

4. The logical variable FINIS controls program termination. The user must add the card:

```
FINIS = TRUE, $
```

as the very last input set. If FINIS is not set, the program will terminate abnormally.

Output

LAKE generates a maximum of four plots per input data set. Each plot contains a set of titles at the top of the plot, x and y axis annotation, x and y axis numeric labels, and a plot legend which specifies, among other things, scale factors for the numeric labels. The parts of a plot are best explained by an example. Consider the first plot in the sample runs. The plot title consists of the three lines:

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE
COMBINED EPILIMNION PRODUCTION OF PHOSPHORUS AND CHLOROPHYLL

The x and y axis annotations are:

EPILIMNION PRODUCTION (KG/M**3-SEC)	(y-axis)
TIME (DAYS)	(x-axis)

The x and y numeric labels, along with the plot legend, enable the user to interpret the plot numerically. For example, a point at the top middle of the plot (designated with a "1" character) is at coordinates (x=.988, y=2.866). Since the scale factor for x is E+02 (10^2) and the scale factor for y is E-11 (10^{-11}), the true coordinates are ($x = 0.988\times10^2$, $y = 2.866\times10^{-11}$) = ($x = 98.8$ days, $y = 0.00000000002866$ kg/m^3-sec).

The last two lines in the plot legend show the number of points mapped to each of 10 z-axis levels (this information is more useful for options which generate a number of different curves on a single page, each one identified by a single z-axis level). In this case, a large number ($>_{\approx}$99) were mapped to z level 0 and show up as blanks, 82 were mapped to z level 1 and show up as 1's, and none were mapped to any other z level.

Restrictions

The user must restrict all input variables according to the range limits listed in the input table, in order to avoid unrealistic physical values.

Error Messages

There are four types of errors which may occur when attempting to execute program LAKE:

1. Syntax errors in the user's input
2. Range check errors
3. Calculation errors
4. Plot parameter errors.

For type 1 and 2 errors, the program flags the error, skips the calculations and plotting, and then reads the next input set. For type 3 errors, the program continues with the calculation and plotting after outputting an error message. For type 4 errors, the program suppresses plotting, outputs an error message, and reads the next data set. For a complete description of type 1 and type 4 error messages and actions, refer to the user's guides for the format free input package and printer plot package, respectively.

Range check errors occur if the range limits set for input variables are exceeded. These messages are of the form:

```
-----ERROR NO. x IN PROG. LAKE-----
     yy----y  OUT OF RANGE
     yy----y  =  dd---d
```

where x is a number from 1 to 13, yy---y is the name of a variable (NDAYS, JSTEP, CLOAD, PLOAD, RPROD, SINK, RHYD, RSED, PSAT, ICHL, IPHOS, ITIME, EDEPTH, HDEPTH, RATIO, or OPLIST) and dd---d is the value.

Calculation errors result when illegal combinations of input variables escape the range checks. These are of the form

```
-----ERROR NO. 14 IN PROG. LAKE-----
     SOLN. DOES NOT CONVERGE AT DAY i, STEP j
     PROCESSING CONTINUES
```

and

```
-----ERROR NO. 15 IN PROG. LAKE-----
     CHL.A OR PHOSPHORUS LTO AT DAY i, STEP j
     PROCESSING CONTINUES
```

Sample Runs

The annotated listing starting on the next page illustrates the control cards and input cards for several sample runs. Each input set is terminated by a $ and generates 0 or more printer plots.

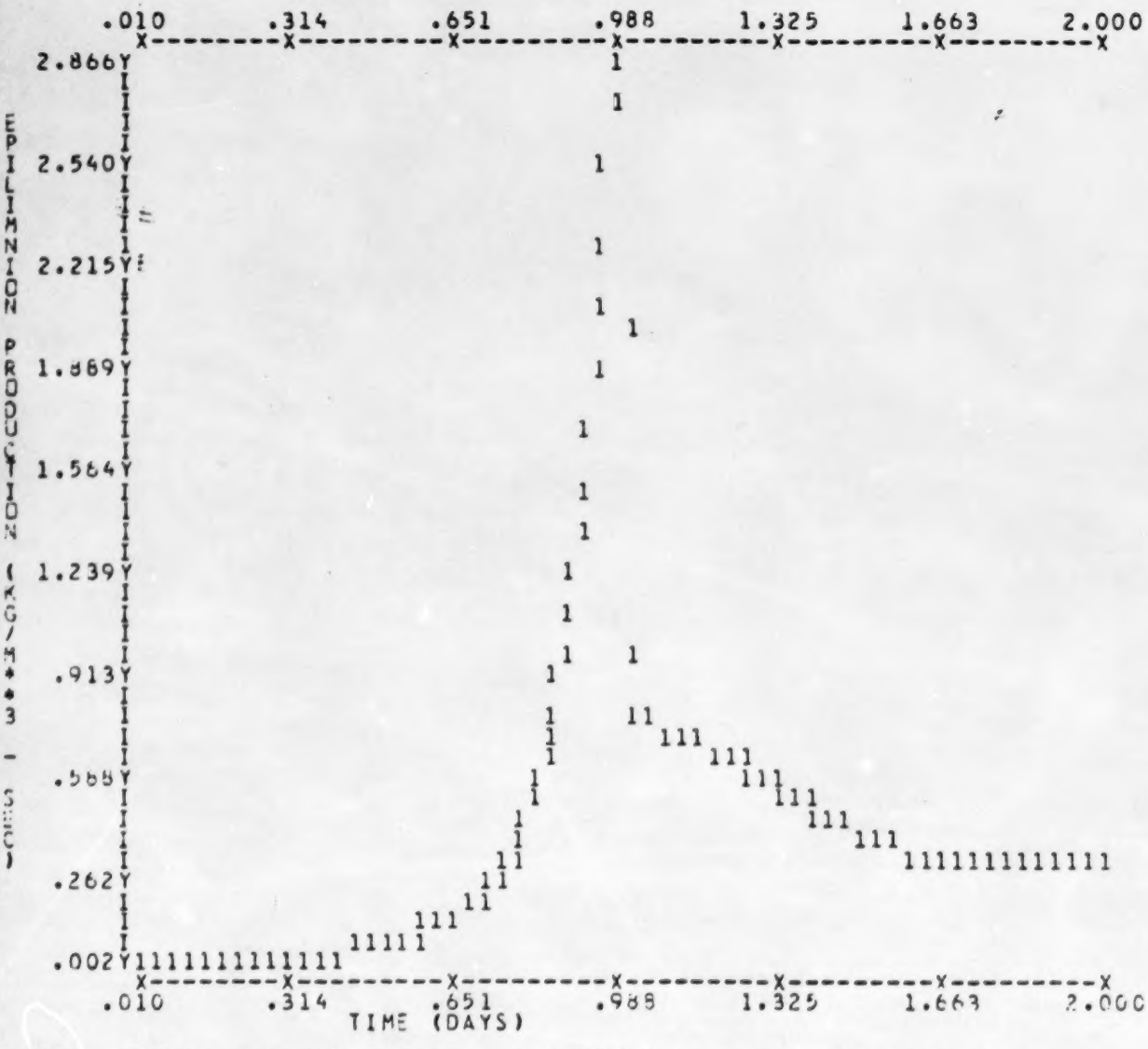
```
XLAKE,CM75000,T30,P5.
ACCOUNT,*******,*******.
COMMENT. ****************************************
COMMENT. *   THE FIRST CARD ABOVE IDENTIFIES    *
COMMENT. * THE JOB, SPECIFIES THE MEMORY        *
COMMENT. * REQUIREMENTS (75000 OCTAL) AND       *
COMMENT. * THE ESTIMATED CENTRAL PROCESSOR      *
COMMENT. * TIME IN SECONDS (30 OCTAL).          *
COMMENT. *   THE ACCOUNT CARD IDENTIFIES        *
COMMENT. * THE BUDGET AND PASSWORD.            *
COMMENT. ****************************************
COMMENT.
ATTACH,LAKE.
MNF,I=LAKE,L=0,E=1,B=BLAKE.
COMMENT. ****************************************
COMMENT. *   THE ATTACH CARD MAKES THE          *
COMMENT. * FORTRAN PROGRAM LAKE  AVAILABLE.     *
COMMENT. *   THE MNF CARD COMPILES THE          *
COMMENT. * PROGRAM AND WRITES ITS BINARY        *
COMMENT. * FORM ONTO FILE BLAKE.                *
COMMENT. ****************************************
COMMENT.
ATTACH,BFF,ID=BFF.
ATTACH,BPR3D,ID=BPR3D.
LOAD,BLAKE,BFF,BPR3D.
EXECUTE.
COMMENT. ****************************************
COMMENT. *   THE ATTACH CARDS MAKE BINARY       *
COMMENT. * SUBROUTINE FILES AVAILABLE --        *
COMMENT. * BFF   = FREE FORM INPUT ROUTINES.    *
COMMENT. * BPR3D = 3D PRINTER PLOT ROUTINES.    *
COMMENT. *   THE LOAD CARD LOADS THE PROGRAM    *
COMMENT. * LAKE  (FILE BLAKE ) INTO MEMORY,     *
COMMENT. * ALONG WITH BFF AND BPR3D.            *
COMMENT. *   THE EXECUTE CARD THEN BEGINS       *
COMMENT. * EXECUTION OF THE PROGRAM LAKE.       *
COMMENT. * INPUT IS HANDLED BY BFF AND          *
COMMENT. * OUTPUT IS PLOTTED BY BPR3D           *
COMMENT. ****************************************
COMMENT.
*EOR
/                                                                              /
/****************************** RUN 1 ***********************************/
/                                                                              /
/ FOR THE FIRST RUN, THE FOLLOWING DEFAULT VALUES ARE ASSUMED --               /
/      EDEPTH = 10                                                             /
/      HDEPTH = 40                                                             /
/      CLOAD  = 0                                                              /
/      PLOAD  = 0                                                              /
/      RPROD  = 2.8E-06                                                        /
/      SINK   = 0                                                              /
/      RATIO  = 3                                                              /
/      RHYD   = 0                                                              /
/      RSED   = 0                                                              /
/      PSAT   = 3.0E-06                                                        /
/      ICHL   = 3.0E-06                                                        /
/      IPHOS  = 7.0E-05                                                        /
/      ITIME  = 0                                                              /
/      JSTEP  = 2                                                              /
/      ECHO   = .T.                                                            /
```

```
/     FINIS  = .F.                                                    /
/     NODFLT = .F.                                                    /
/                                                                     /
/ THE PLOT OPTIONS ARE:                                              /
      OPLIST = 1,2,3,4,
/ THE CALCULATION IS TO RUN FOR 200 DAYS                             /
      NDAYS  = 200, $
/                                                                     /
/******************************** RUN 2 ***********************************/
/                                                                     /
/ FOR THE SECOND RUN, THE DEFAULTS ARE THE SAME AS FOR RUN 1,        /
/ WITH THE FOLLOWING EXCEPTIONS --                                   /
/ PRODUCTION RATE                                                    /
      RPROD  = 8.E-6,
/ SINKING SPEED                                                      /
      SINK   = 6.E-6,
/ SEDIMENTATION RATE                                                 /
      RSED   = 1.E-5,
/ THE CALCULATION WILL BE RUN FOR 200 DAYS                           /
      NDAYS  = 200, $
/                                                                     /
/******************************** RUN 3 ***********************************/
/                                                                     /
/ ONLY THE FOLLOWING VALUES ARE CHANGED FROM THE DEFAULTS OF RUN 1 -- /
/ PRODUCTION RATE                                                    /
     RPROD  = 2.8E-6,
/ PHOSPHORUS HALF-SATURATION CONSTANT                                /
     PSAT   = 3.1E-5,
/ INITIAL CHLOROPHYLL-A CONCENTRATION                                /
     ICHL   = 2.0E-5,
/ INITIAL PHOSPHORUS CONCENTRATION                                   /
     IPHOS  = 7.0E-5,
/ THE CALCULATION WILL BE DONE FOR 200 DAYS                          /
     NDAYS  = 200, $
/                                                                     /
/***************************** TERMINATE PROGRAM **********************/
/                                                                     /
      FINIS  = .T., $
*EOR
*EOF
```

PROGRAM -LAKE- READY FOR INPUT

```
/                                                                              /
/*********************************** RUN 1 ************************************/
/                                                                              /
/  FOR THE FIRST RUN, THE FOLLOWING DEFAULT VALUES ARE ASSUMED --              /
/       EDEPTH = 10                                                            /
/       HDEPTH = 40                                                            /
/       CLOAD  = 0                                                             /
/       PLOAD  = 0                                                             /
/       RPROD  = 2.8E-06                                                       /
/       SINK   = 0                                                             /
/       RATIO  = 3                                                             /
/       RHYD   = 0                                                             /
/       RSED   = 0                                                             /
/       PSAT   = 3.0E-06                                                       /
/       ICHL   = 3.0E-06                                                       /
/       IPHOS  = 7.0E-05                                                       /
/       ITIME  = 0                                                             /
/       JSTEP  = 2                                                             /
/       ECHO   = .T.                                                           /
/       FINIS  = .F.                                                           /
/       NODFLT = .F.                                                           /
/                                                                              /
/  THE PLOT OPTIONS ARE:                                                       /
/       OPLIST = 1,2,3,4,                                                      /
/  THE CALCULATION IS TO RUN FOR 200 DAYS                                      /
/       NDAYS  = 200, $
```

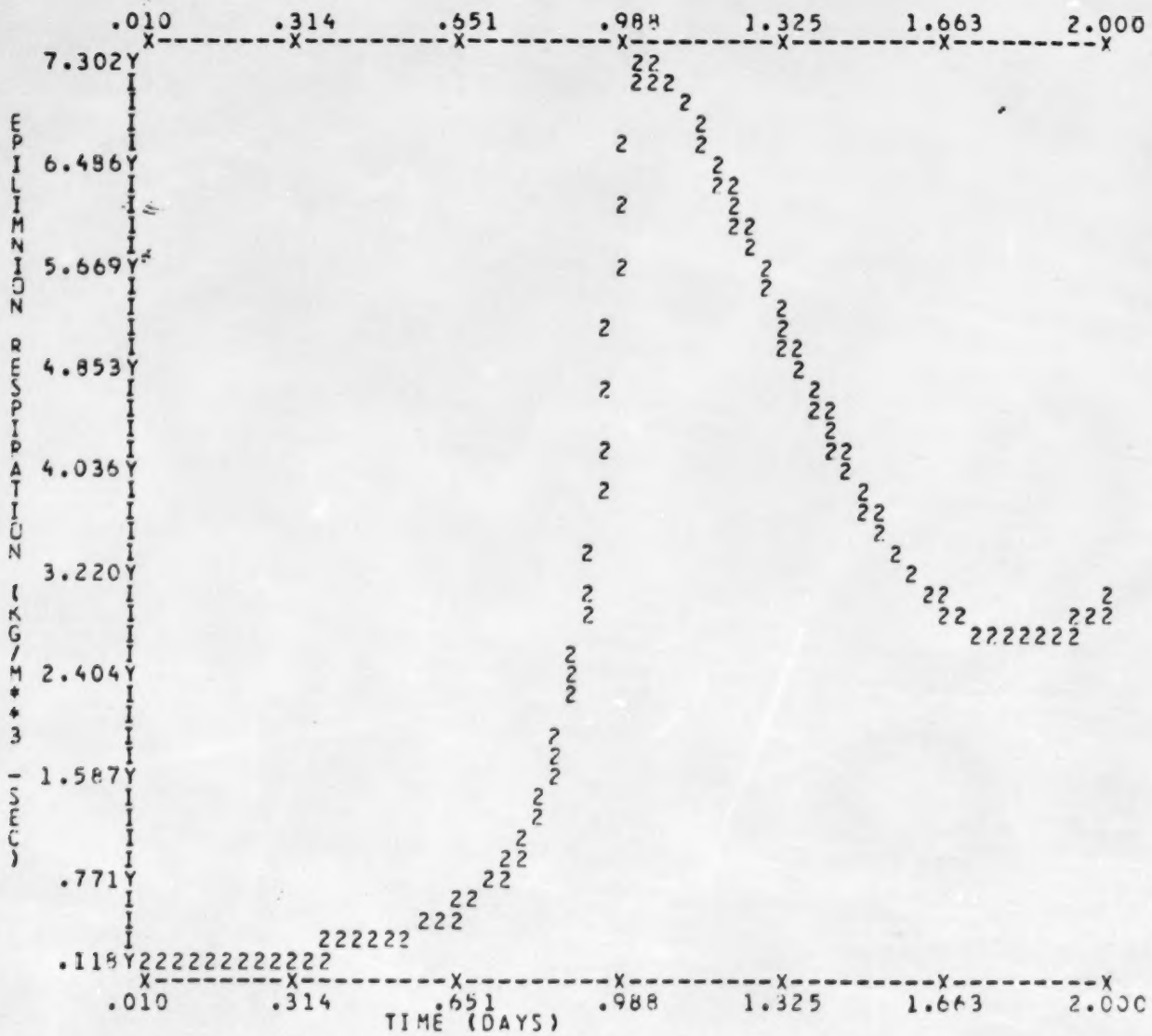
MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE
COMBINED EPILIMNION PRODUCTION OF PHOSPHORUS AND CHLOROPHYLL



SCALE FACTORS • X-AXIS: E+02 Y-AXIS: E-11 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(82), 2.000(0), 3.000(0), 4.000(0)
Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE

EPILIMNION RESPIRATION IN UNITS OF CHLOROPHYLL -A-



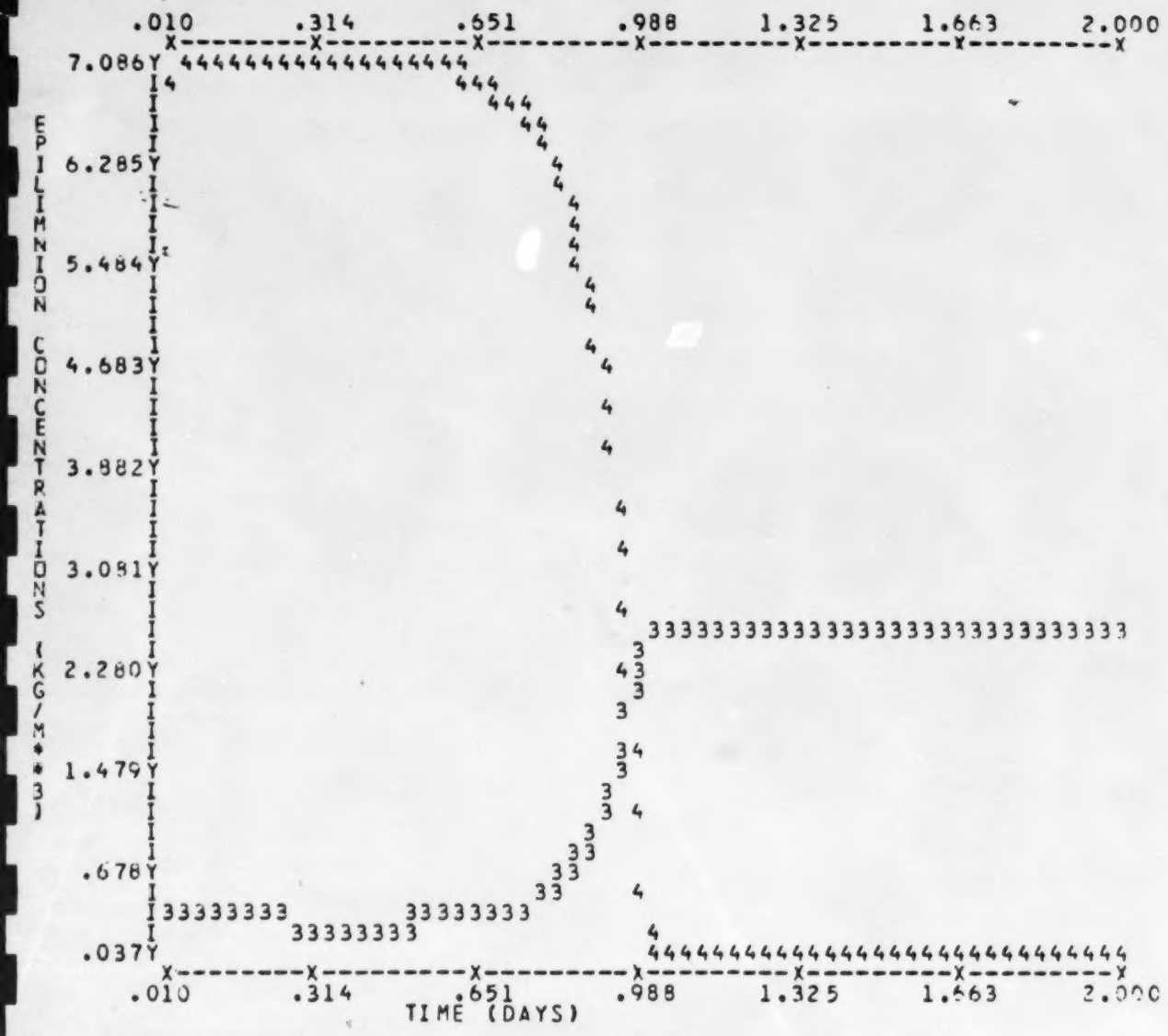
SCALE FACTORS = X-AXIS: E+02 Y-AXIS: E-12 Z-AXIS: E+00

Z0-Z4= 0(-9), 1.000(0), 2.000(96), 3.000(0), 4.000(0)

Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE

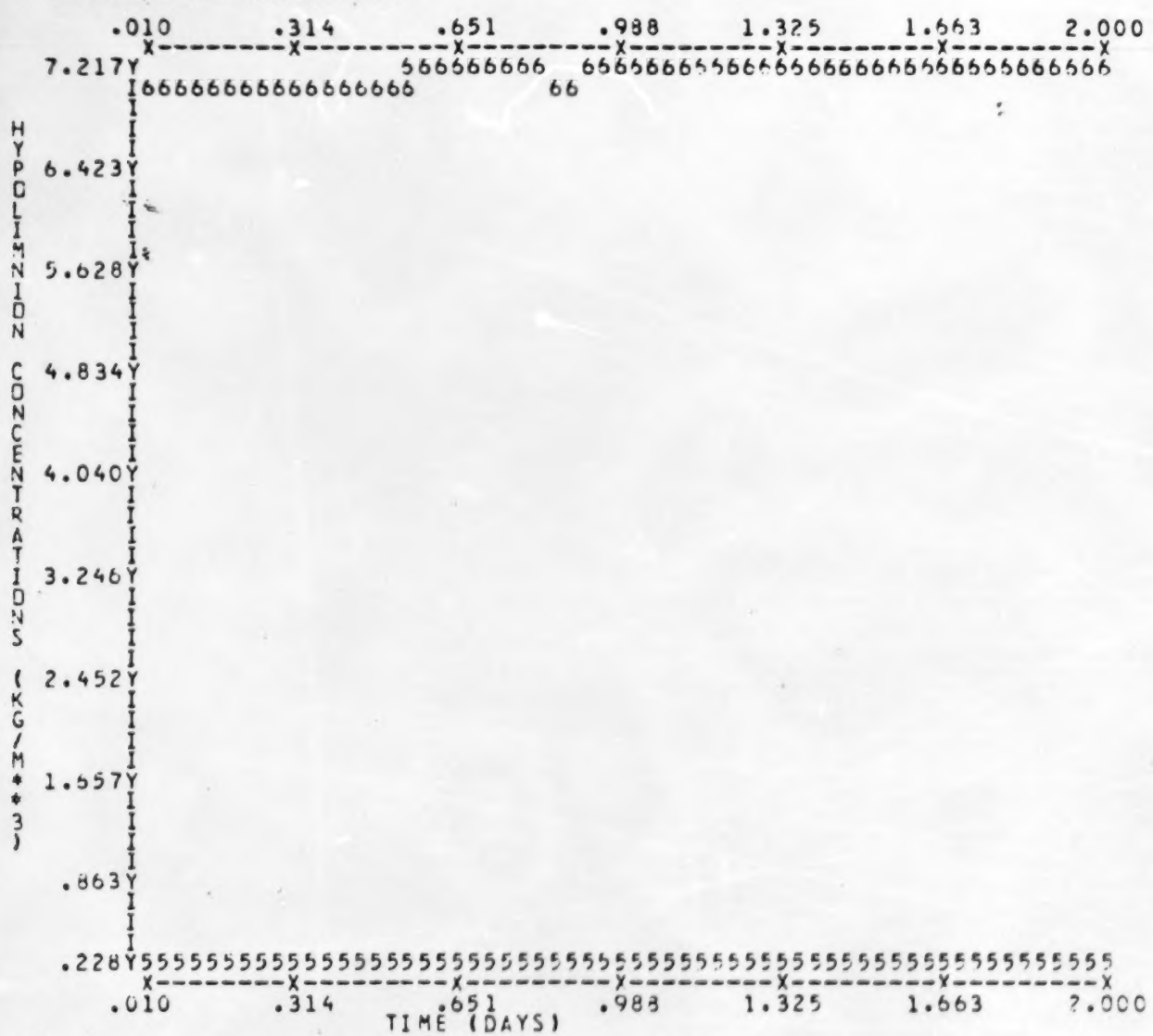
EPILIMNION CONCENTRATION OF CHLOROPHYLL -A- (CURVE 3)
AND PHOSPHORUS (CURVE 4)



SCALE FACTORS = X-AXIS: E+02 Y-AXIS: E-05 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(0), 2.000(0), 3.000(69), 4.000(78)
Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE

HYPOLIMNION CONCENTRATION OF CHLOROPHYLL -A- (CURVE 5)
AND PHOSPHORUS (CURVE 6)



SCALE FACTORS = X-AXIS: E+02 Y-AXIS: E-05 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(0), 2.000(0), 3.000(0), 4.000(0)
Z5-Z9= 5.000(60), 6.000(61), 7.000(0), 8.000(0), 9.000(0)

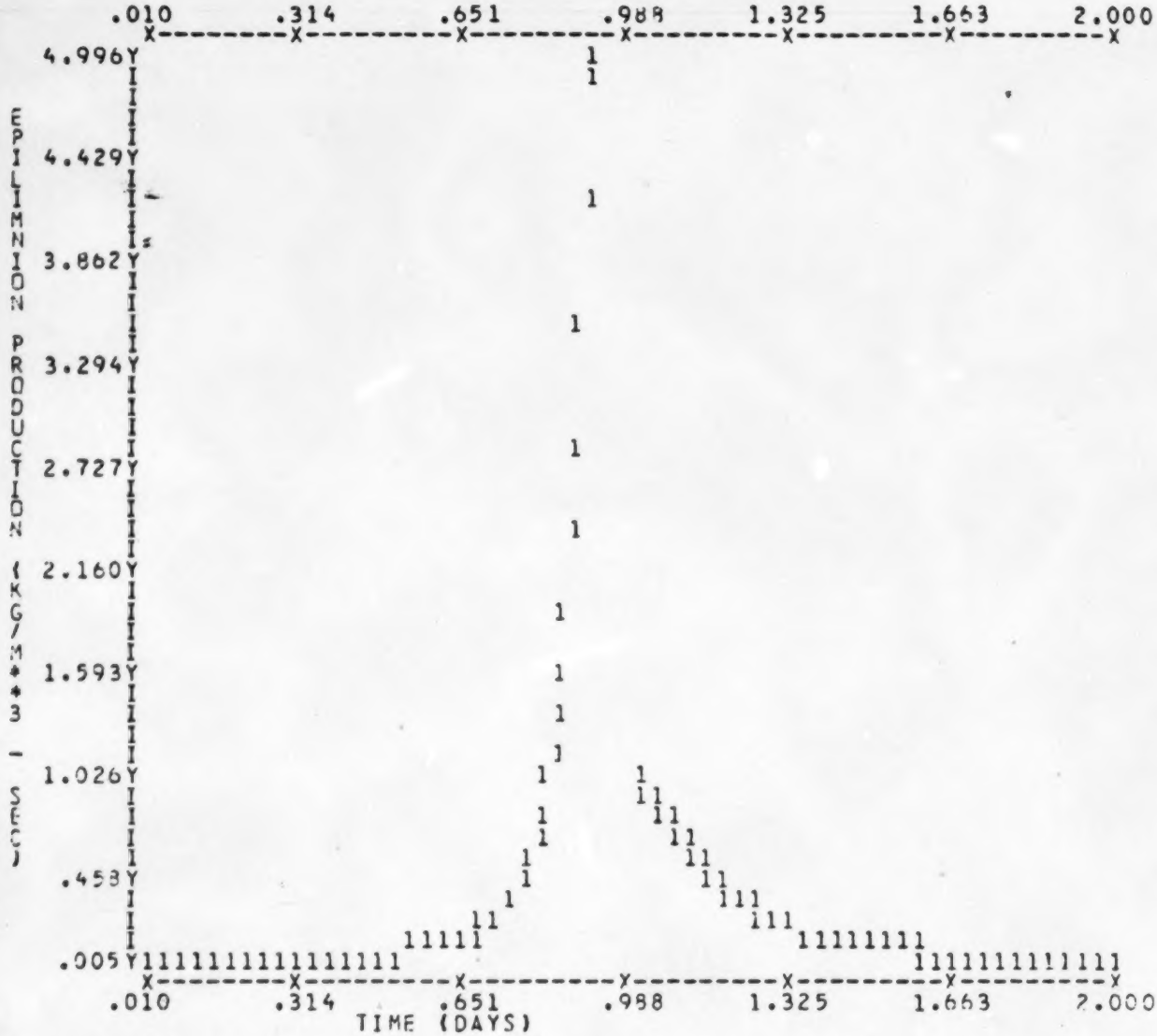
OGRAM -LAKE- READY FOR INPUT

```
/                                                                    /
/********************************* RUN 2 ***********************************/
/                                                                    /
/ FOR THE SECOND RUN, THE DEFAULTS ARE THE SAME AS FOR RUN 1,        /
/ WITH THE FOLLOWING EXCEPTIONS --                                   /
/ PRODUCTION RATE                                                    /
      RPROD  = 8.E-6,
/ SINKING SPEED                                                      /
      SINK   = 6.E-6,
/ SEDIMENTATION RATE                                                 /
      RSED   = 1.E-5,
/ THE CALCULATION WILL BE RUN FOR 200 DAYS                           /
      NDAYS  = 200, $
```

--ERROR NO. 14 IN PROG. LAKE----
SOLN. DOES NOT CONVERGE AT DAY 94, STEP 1
PROCESSING CONTINUES

```
--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  94, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  95, STEP   1
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  95, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  96, STEP   1
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  96, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  97, STEP   1
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  97, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  98, STEP   1
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  98, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  99, STEP   1
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY  99, STEP   2
  PROCESSING CONTINUES

--ERROR NO. 14 IN PROG. LAKE----
  SOLN. DOES NOT CONVERGE AT DAY 100, STEP   1
  PROCESSING CONTINUES
```

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE
COMBINED EPILIMNION PRODUCTION OF PHOSPHORUS AND CHLOROPHYLL

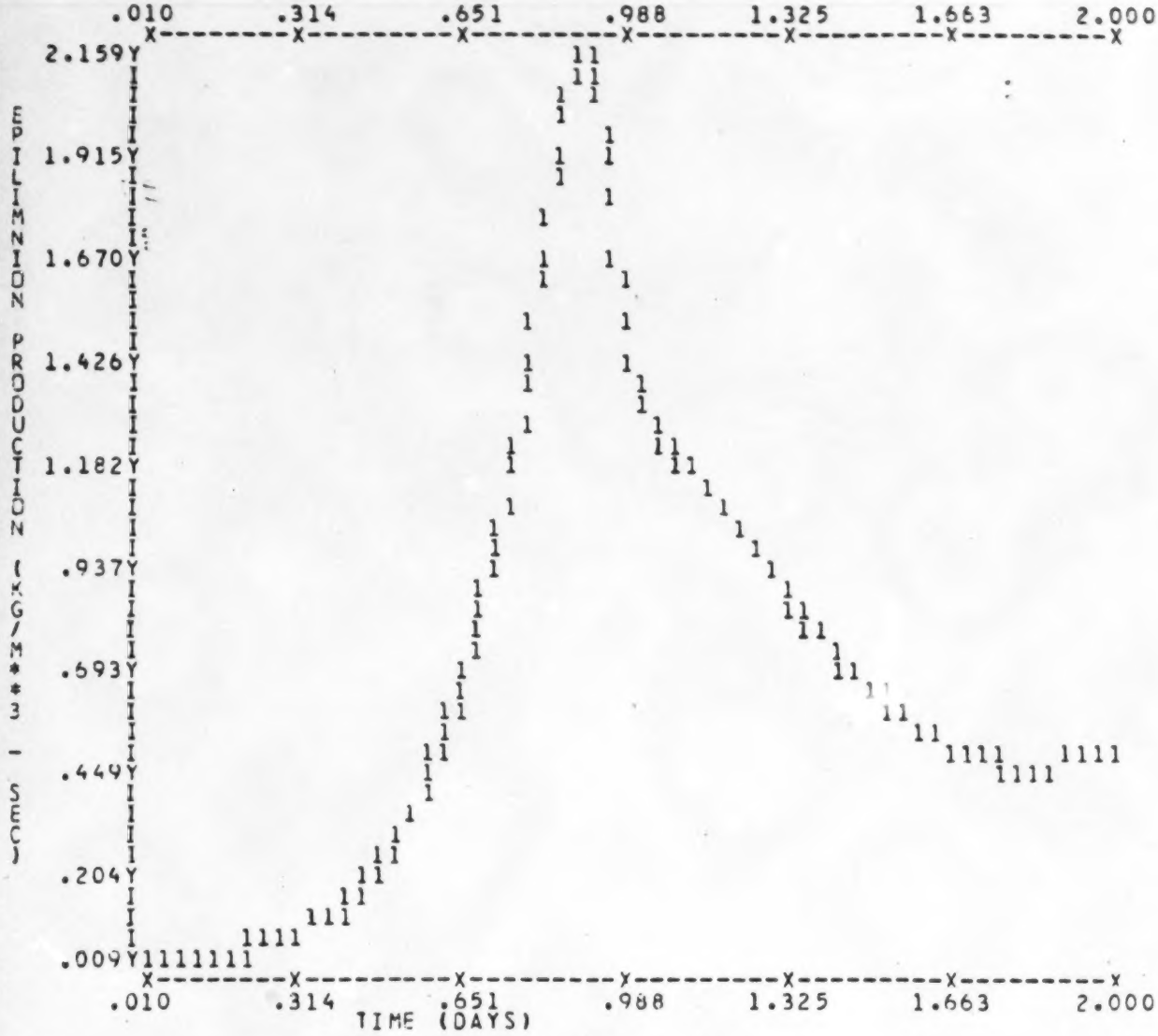


SCALE FACTORS = X-AXIS: E+02 Y-AXIS: E-11 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(77), 2.000(0), 3.000(0), 4.000(0)
Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

UGRAM -LAKE- READY FOR INPUT

```
/                                                                    /
/********************************* RUN 3 ***********************************/
/                                                                    /
/ ONLY THE FOLLOWING VALUES ARE CHANGED FROM THE DEFAULTS OF RUN 1 -- /
/ PRODUCTION RATE                                                    /
     RPROD  = 2.8E-6,
/ PHOSPHORUS HALF-SATURATION CONSTANT                                /
     PSAT   = 3.1E-5,
/ INITIAL CHLOROPHYLL-A CONCENTRATION                                /
     ICHL   = 2.0E-5,
/ INITIAL PHOSPHORUS CONCENTRATION                                   /
     IPHOS  = 7.0E-5,
/ THE CALCULATION WILL BE DONE FOR 200 DAYS                          /
     NDAYS  = 200, $
```

MODEL OF CHEMICAL CONCENTRATIONS IN A TEMPERATURE STRAT. LAKE
COMBINED EPILIMNION PRODUCTION OF PHOSPHORUS AND CHLOROPHYLL



SCALE FACTORS = X-AXIS: E+02 Y-AXIS: E-11 Z-AXIS: E+00
Z0-Z4= 0(-9), 1.000(-9), 2.000(0), 3.000(0), 4.000(0)
Z5-Z9= 5.000(0), 6.000(0), 7.000(0), 8.000(0), 9.000(0)

OGRAM -LAKE- READY FOR INPUT

/
/********** TERMINATE PROGRAM **********/
/

FINIS = .T., $

OGRAM -LAKE- TERMINATED

REFERENCES

Gales, L.E. 1978. User's guide for subroutine PRNT3D. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle.

Gales, L.E. and L. Anderson. 1978. User's guide for subroutine FFORM: a format free input system. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle.